THE EFFECTS OF NUTRITIONAL FACTORS ON MICROBIAL AGGREGATION[1]

G. B. CALLEJA and BYRON F. JOHNSON

Division of Biological Sciences, National Resesearch Council of Canada, Ottawa, Ontario, Canada K1A OR6.

[1]N.R.C.C. No. 16394

Microbial aggregation is an ill-defined subject. Poor definition, however, has not prevented earlier attempts to collect the scattered literature on the subject.[1-5] Before we present our compilation, we shall make our own brave attempt at definition.

Aggregation may be defined as the gathering together of wholes to form a bigger whole. The resultant whole may also be called an aggregation. The clumping of cells is aggregation. The clump is an aggregation of cells -- or an aggregate. In the first sense, aggregation is a process, a function. In the second, it is a product, a structure.

The wholes and the gathering together may be physical or merely conceptual. A compilation such as this subsection is therefore an aggregation. A cell is an aggregation of molecules. The mathematical operation of addition is aggregation. The resultant sum is an aggregation too. And so is any collective noun or pronoun. However, we are not concerned here with either numerical manipulation or grammar (although both are involved), but the palpable -- specifically, with the aggregation of microbial cells. A chain of streptococci can be considered an aggregation. But even in the conceptual sense, the process of chain formation in streptococci is not aggregation. It is called cell division or even cell multiplication. Aggregation is addition -- arithmetically and rhetorically.

With the above in mind and with the assumption that aggregation is both a fundamental function and a fundamental

structure in biology, we define cell aggregation as the gathering together of cells to form fairly stable, contiguous, multicellular associations under physiological conditions. In the literature, it is also known as adhesion, adherence, agglomeration, agglutination, association, autoagglutination, clumping, coagulation, cohesion, flocculation, flocculence, isoagglutination. The resultant structure is also called aggregate, agglutinate, clump, cluster, coagulum, coremium, floc, pellet, pellicle, plasmodium, rhizomorph, sclerotium, slime, slug, strand, stroma, synnema.

The definition has two main elements: physical movement and stable many-cell contacts. Both must be present in any system of cell aggregation. Movement may be either directed, as is chemotaxis in the cellular slime molds; or random, as is Brownian collision in the flocculation of brewers yeast.

Contacts must be intercellular; a monolayer of cells on glass fails to satisfy the definition. Moreover, contacts must be multicellular; the minimally plural condition is not sufficient. Our reason here is practical rather than grammatical, for if we were to include pair-formation (mechanistically, but not formally by our definition, an aggregation), then all conjugation systems would have to be included -- and that would hardly constitute a manageable list. A lower limit of ten cells appears to us as a reasonable, albeit arbitrary, number for a minimal group.

Contacts may be transient, but must endure long enough and be strong enough to be experimentally definable.

An aggregation system that does not lead to cell fusion or conjugation must be able to withstand Brownian forces under physiological conditions. For example, a sediment of non-flocculent yeast cells disperses as a fairly homogeneous suspension in wort. That of flocculent cells does not.

We list below excluded phenomena which can be (and have been in the literature) mistaken for cell aggregation systems. For convenience, these are grouped as follows:

1) Multicellular condition due to failure of progeny to separate after cell division -- chain, filament, mycelium, pseudomycelium, fruiting body, plasmodium, colonial form, coenocyte, syncytium.

2) Tropic response without subsequent stable association -- chemotaxis, phototaxis, aerotaxis, swarm, pellicle.

3) Association due to growth under non-dispersive conditions -- colony on solid medium, focus of infection, sediment, pellet, bloom, pellicle.

4) Association with non-cellular objects -- phage adsorption, adsorption onto solids, adhesion to glassware, adherence, stickiness.

5) Interaction short of the multicellular condition -- pair formation, copulation, conjugation, heterokaryon formation, palmella formation.

6) Aggregation provoked under obviously non-physiological conditions -- precipitation, coagulation, agglutination, sedimentation, and denaturation by strong acids and alkalis, organic solvents, heat, desiccation, dehydration, centrifugation, lyophilization.

7) Aggregation provoked by substances not usually found in the culture medium nor produced by the organism -- agglutination, flocculation, sedimentation provoked by antibodies, agglutinins (e.g., concanavalin A, wheat germ agglutinin, ricin), synthetic polymers (e.g., polyethyleneimine, polylysine), native or denatured enzymes (e.g., lysozyme, ribonuclease), serum proteins (e.g., albumin), artificial flocculants (e.g., bentonite, undefined clays, boric acid).

From the definition and the enumerated exclusions, we derive criteria for making a list of aggregation systems (Table 1). To be entered, an aggregation system must be 1) active (it must be shown that there is a change from a free-cell condition to an aggregated condition), 2) inducible (a physiological situation must be found in which aggregation is absent), 3) stable (as an aqueous suspension), 4) intercellular (adhesion or adsorption to non-cellular surfaces is discounted), 5) multicomponent (at least ten cells), 6) spontaneous (compatible with the life cycle of the organism, not due to unphysiological provocations). In addition, for our present purpose, the system must have been investigated from a nutritional vantage point.

Our exigent and expedient limitations notwithstanding, cell aggregation remains a widespread phenomenon in the microbial world. Our list includes bacteria, yeasts, cellular and acellular slime molds, filamentous fungi, algae, and protozoa. It is representative rather than comprehensive, for some known systems are not discussed nutritionally in the

literature. The great majority still await scholarly attention.

Yeast flocculation has been the object of study since the days of Pasteur because of its obvious importance in the brewing industry. Lately, plaque formation in streptococci has received much attention because of its possible relation to cariogenesis and periodontal diseases. Other complex aggregation systems, not yet amenable to nutritional experimentation and therefore not included in our list, are studied for their central role in sewage treatment, infection, soil conditioning, and ecology.

The significance of aggregation as a biological phenomenon, however, far outweighs its contribution to worldly affairs. Aggregation in the cellular slime molds has attracted many, partly because it is a prelude to morphogenesis; sexual agglutination in yeasts, partly because it is a prelude to sex; and stroma formation in filamentous fungi, partly because it is a mechanism for survival. Indeed, most of the better studied aggregation systems may be grouped into one of these three teleological categories, depending upon a system's apparent primary reason for being. Some, or possibly most, may embrace all three: the categories are not mutually exclusive. However classified, an aggregation system is a differentiation system, a developmental system, simply because it is part of the life cycle of an organism, and because it is inducible.

As would be expected of a developmental system, cell aggregation is greatly influenced by nutritional conditions.

The organisms in our list are as diverse as are the mechanisms by which the multicellular condition is achieved. Consequently, the nutritional factors that influence the systems are diverse -- and their influences are occasionally contrary.

The difficulties encountered in the making of a compilation of this sort derive from various sources as well. One difficulty is inherent to nutritional studies of a function. What is a nutritional factor? Nutrition, being a part of physiology, can be extended to embrace a good deal of physiology. Depending upon the response of an organism to an exogenous substance, a nutritional investigation may remain as such or may become a metabolic, pharmacological, or toxicological study. There is even the danger that it may become molecular biology.

Another difficulty is inherent to cellular systems: there is no hard line between internal consumption and external application, between what goes into metabolism and what does not, what is dietary and what is not. Are ions which simply help stabilize flocs nutritional factors? Otto Loewi once defined a drug as a substance which when injected into an animal results in a paper. For the moment, we take a cue from him and define a nutritional factor as a substance which when introduced into the culture medium secures for itself an entry in our list. Thus, an arbitrariness in the choice of entries. We shall try to justify our choices a little later.

Another difficulty stems from the fact that sometimes aggregations are not the most conspicuous phenomenon in a complex series of events. This has occasionally led to aggregation being ignored. When aggregation merits more than

a casual observation, what often is scored are the events which follow (conjugation, fruiting-body formation) or the events preceding (chemotaxis, gamete formation) or the associated events (the development of competence for transformation, the development of competence for conjugation), rather than aggregation *per se* or the competence to aggregate.

The ideal would be to assay for competence to aggregate rather than scoring aggregation itself or its associated activities, for quite often, aggregation is artificially provoked and manipulated. For example, the mixing of mating types is often achieved by manual transfer of a culture from one container to another. But the compiler's job is not writing prescriptions.

Several of the systems included in the list seem unexpected and need introductions. These are: mating-aggregate formation during conjugation in *Escherichia coli*, agglutination associated with transformation competence in bacteria, mating reaction in *Euplotes*, and mating reaction in *Blepharisma*. Bacterial conjugation has been considered as simple pair-formation for a number of decades. Recently, however, it has been shown convincingly that the mating structure is an aggregate.[6] Genetic transformation in bacteria is a phenomenon known even longer. But only in this decade has it been reported that associated with competence for transformation is an agglutination reaction.[7-9] The mating reactions in *Euplotes* and *Blepharisma*, unlike those in *Paramecium* and *Chlamydomonas*, have for many years been known to be so weak that they have been assumed to be mere gametangial pairing. Ways of eliciting the agglutination reactions have been found recently.[10-11] However, we have not

come upon any report as to the aggregating capacity of Tetrahymena, and thus its absence from the list. When the preferred orientations of other seemingly reluctant organisms are uncovered, the list will become much longer.

As much as possible, we have retained the terminologies used by the original authors. Where there is no agreement as to the proper terminology among several schools in a particular system, we have chosen the more popular nomenclature. Where there is no particular terminology advanced, we have taken the liberty of assigning a descriptive title as a way of identifying it and preventing its being confused with similar or related phenomena.

Rather than make a detailed commentary on each entry under nutritional condition, we have simplified the annotation by classifying the observed responses into three classes. The first is positive effect, i.e, the specified nutritional condition stimulates, enhances, hastens, induces, supports, magnifies, increases, intensifies, stabilizes, or is required; in short, it is favorable to aggregation. The second is negative, i.e., the condition depresses, inhibits, delays, represses, antagonizes, prevents, decreases, diminishes, attenuates, destabilizes; in short, it is unfavorable. The third is indifferent, i.e, the nutritional condition exerts no significant influence on aggregation.

We tried as much as possible to exclude all well known metabolic inhibitors such as cyanide, the antibiotics, and other drugs. When a condition was found to be inhibitory, we made sure that it did not inhibit growth as well (or other gross cellular functions). When a listed substance or a nutritional

conditions inhibits aggregation, either the substance is not known as a metabolic inhibitor, or is found in the culture medium as an ingredient or as a metabolite, or because others have reported exactly opposite results.

Some known inhibitors are included because they stimulate aggregation. All stimulating substances are included regardless of their repute, except when considered as outright non-biological.

Ions, whatever their modes of action, are included for they are usually added to or found in a culture medium. Secreted products of the organisms, such as sex factors, competence factors, and hormones, are included for the same reason.

We have limited the ineffectual entries to conditions similar or related to those which yielded negative or positive effects, or are expected by reputation to yield negative or positive effects. Had we not thusly limited the entries, the list would have been much longer, but probably not much more useful.

Unless a finding has been in obvious error -- conceded later by the original observers or proved decisively by others -- we give the benefit of the doubt to the original authors. Thus, disputed observations have a place in the list.

Long as the list is, and varied as are the nutritional conditions which stimulate or inhibit aggregation, only a few generalizations can be made. As a requirement for induction, starvation or semi-starvation -- general or for some specific nutrient -- is rather common among the protozoa and algae, the cellular and acellular slime molds, the myxobacteria, and the yeasts. It is rare among the other bacteria and the

filamentous fungi. In general, conditions that favor growth are inimical to aggregation. On the other hand, the induction of competence to aggregate is apparently energy-requiring. Complete starvation may serve as a trigger for development, but only if the requirement for energy can be met endogenously. This situation pertains to gametogenesis in the algae and fruiting-body formation in the cellular slime molds. What probably happens is that nutrient depletion causes a general derepression which somehow turns on the developmental program.

Oxygen appears to promote aggregation in some systems. When it is required, as in the fission yeast, it may reflect simply the requirement for energy-generating mechanisms which are repressed during anaerobiosis.

Although some ions may be specifically required for induction of some aggregation systems (for instance, in Hansenula or Escherichia coli), most ions probably act merely as gegenions to effect the formation and the stabilization of aggregated structures derived from already competent cells. The divalent cations are preferred generally, and among them, Ca^{2+} and Mg^{2+} are quite often implicated. Some ecstatic claims will just have to be taken with a grain of salt.

A number of systems appear to be mediated by hormones. The word is used loosely in the present context. These are the sex factors, chemotactic substances, and the gamones. When cell-free culture fluids show some aggregation-promoting activity, diffusible metabolites are often suspected and looked for.

Diffusible factors might be active in all systems where coordination among components is the sine qua non for success -- as in conjugation between heterothallic cells and in slug formation -- and where intercellular contacts are rather weak. They do not seem to be operative in systems that involve particularly strong, stable, and durable interaction. Possibly their effects are masked by the vigor of the reaction. But then again, the latter systems may leave encounters to chance and rely upon the strength and the specificity of the interaction for instant recognition and coordination -- instead of pre-encounter telecommunication. Diffusible factors appear to be the solution to situations which involve directed movement rather than stochastic processes. In a Brownian environment, where movement is random, there is room for trial and error and a diffusible factor is of little advantage. Instead, surface-bound recognition sites are certain to be more fruitful.

Sugars have been studied as carbon and energy sources, as potential competitors for putative receptor sites on the cell surface, and as precursors of repression. They have not been found to be specific inducers, except in the case of dextran-mediated agglutination in streptococci. When inhibitory, their effect is likely to be a consequence of their role in catabolite repression.

Positive effects of nucleotides have been reported far more frequently. Cyclic AMP is a chemotactic agent in Dictyostelium, but has been found ineffectual in Polysphondelium -- illustrating the highly specific nature of elaboration of and

sensitivity to diffusible factors. It has been reported to be active in some other systems. Furthermore, the nucleoside triphosphates have been found to promote aggregation in the cellular slime molds.

The results of studies with amino acids and peptides as a group of nutrients are varied and contradictory. Some amino acids have been claimed to be specific inducers or inhibitors. Further studies under more defined cultural conditions may reveal that these amino acids, when inhibitory, merely act as agents of a more general metabolic repression and, when stimulatory, as components of other general functions, such as protein synthesis, which may be required for the synthesis of aggregation molecules.

Except possibly for folic acid in the cellular slime molds, the vitamins, purines, pyrimidines, intermediary metabolites, and the steroids have been a disappointment. Lipids have been virtually ignored.

Indeed, there are very few meaningful and trustworthy observations regarding nutritional requirements for aggregation. Cyclic AMP as a chemotactic agent in the slime molds may stand the test of further probing, so may nitrogen starvation as a gametogenic condition for Chlamydomonas and sucrose as an inducer of dextran-mediated agglutination in streptococci. That any substance works at all either to promote or to inhibit aggregation is probably good enough -- if the goal of a nutritional study is simply to define conditions for maximal or minimal aggregation.

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Table 1. The effects of nutritional factors on microbial aggregation

System & Review References	Nutritional Condition	Positive	Negative	Indifferent	References
I. Bacteria					
1) Mating-aggregate formation during conjugation in Escherichia coli[6,12-14]	Cell extract		X		15
	Mg^{2+}, Ca^{2+}			X	16
Donor cell	Anaerobiosis	X			17,18
	Starvation		X		17,18
	Rich medium	X			17,18
	Glucose as C source	X			17,18
	Casamino acids	X			17,18
	Growth factors	X			17,18
	Zn^{2+}		X		6,16
Recipient cell	Aeration	X			17,18
	Zn^{2+}	X			19
2) Star formation in Pseudomonas, Rhizobium, Agrobacterium	Nutrient broth	X			20-22
	Peptone + yeast extract	X			23
	Minimal medium		X		20
3) Pellicle formation in fimbriated bacteria[24]	Aerobic + static culture	X			25-31
	Nutrient broth	X			25-28,32

System & Review References	Nutritional Condition	Positive	Negative	Indifferent	References
	D-glucose, L-sorbose			X	27
	D-mannose		X		26,27
	α-methyl mannoside		X		27,29
4) Agglutination associated with transformation competence in bacteria[7-9,33-39]					
a) Streptococcus	Peptides	X			40
	Free amino acids	X			40
b) Pneumococcus	No energy source		X		41
	Glucose or sucrose as C source	X			41,42
	Glutamine	X			41,42
	Leucine, valine	X			41,42
	Isoleucine	X			41
	Arginine	X			42
	Glycine	X			43
	Maleate		X		44
	Uridine	X			41
	Choline	X			41
	Mg^{2+}	X			41

System & Review References	Nutritional Condition	Positive	Negative	Indifferent	Reference
c) Bacillus	Aeration	X			45,46
	Complex, rich medium		X		47,48
	Yeast extract	X			46,47,49
	Casein hydrolysate	X			47,49
	Casein hydrolysate		X		48,50
	Glucose as C source	X			49
	Sucrose as energy source	X			51
	Acetate, succinate, glycerol as energy source		X		51
	Pyruvate, lactate, glucose compared as energy sources			X	45
	Ammonium salt as N source	X			49
	Additional N as nitrate or ammonium salt	X			51
	Amino acids		X		49
	Histidine	X			49-53
	Arginine	X			50,51
	Arginine, histidine at doubling time = 2.5h			X	54
	Arginine, histidine at doubling time = 6.5h	X			54
	Alanine, glutamic acid at doubling time = 2.5h	X			54
	Alanine, glutamic acid at doubling time = 6.5h		X		54
	Alanine, glutamic acid		X		47,50,53
	Tryptophan	X			47,49,51,53

System & Review References	Nutritional Condition	Positive	Negative	Indifferent	Reference
	Threonine, glycine, valine, aspartic acid, lysine, methionine, phenylalanine, cystine, serine, tyrosine	X			50,51
	Phenylalanine, cystine, serine, tyrosine		X		50
	Leucine, isoleucine, proline, D-lysine, diaminopimelic acid		X		50
	Indole	X			47,49
	β-mercaptoethanol	X			49,52,55
	Phosphate		X		55
	EDTA	X			49
	Mg^{2+}	X			45,47,52,53,55
	Cu^{2+}		X		45,48,49,52
	Fe^{2+}, Mn^{2+}		X		51
	Ba^{2+}, Sr^{2+}, Ca^{2+}	X			45
	Ni^{2+}, Zn^{2+}		X		45
d) Haemophilus	Anaerobiosis	X			56
	Glucose			X	57
	Glycerol		X		56
	Lactate	X			56,58
	Fumarate			X	56
	α-ketoglutarate			X	57

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
	Aspartic acid, glutamic acid	X			57,59
	Valine		X		59
	Cystine, arginine, citrulline	X			59
	Other amino acids			X	57
	Cyclic AMP	X			60
	Cyclic GMP, ATP, ADP, AMP			X	60
	Inosine	X			58
	Inosine		X		56,61
	Uracil		X		56
	Vitamin mixture (NAD + thiamine + pantothenate + uracil + hypoxanthine)		X		59
	NAD		X		56
	Thiamine			X	56
	Pantothenate			X	56
	Salts (Ca, Mg, NaCl)	X			59
	Ca^{2+}, Mg^{2+}	X			57,59
5) Plaque formation and agglutination in *Streptococcus mutans*[62]	Dextran	X			62-65
	Sucrose	X			62,63,65-69
	Fructose		X		65
	Other sugars & polysaccharides (glucose, fructose, dextrin, agar, agarose, inulin, mannitol, sorbitol)		X	X	63-65

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
6) Clumping in Corynebacterium xerosis	Hydrogen gas		X		70
	Nitrogen gas			X	70
	Inorganic salts	X			70
7) Cell clumping in Nocardia corallina	Nutrient agar + fructose	X			71
8) Aggregation in myxobacteria[72-74]	Starvation	X			75
	Nutrient-rich medium		X		76-80
	Peptone		X		76,81
	Hydrolysed casein, amino acids		X		81-83
	Limited concentration of required amino acids (phenylalanine, isoleucine, leucine, methionine, valine)	X			83
	Phenylalanine, tryptophan		X		75, 81-84
	Methionine		X		83
	Steroids	X			85
	Phosphate			X	86
	Divalent cations (Ca^{2+}, Mg^{2+}, Sr^{2+})	X			86
	Ca^{2+}	X			86,87
	K^{+}, Na^{+}	X			86

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
II. Mycetozoa					
1) Aggregate growth in Physarum	Nutrient (dead bacteria) depletion	X			88,89
	Amino acids	X			90
	L-tryptophan	X			90
	Cyclic AMP			X	90
2) Aggregation in cellular slime moulds[91-122]					
a) Dictyostelium	Oxygen	X			123,124
	Nitrogen gas		X		124
	Nutrient (live or dead bacteria) depletion	X			101,104-109,111,113, 115-118,120,122,125
	Bacterial extract	X			126,127
	Growth medium		X		116
	Yeast extract			X	116
	Peptone		X		116
	Bovine serum albumin	X			128
	Glucose	X			129-131
	Glucosamine		X		132
	Glycerol		X		125
	Citrate		X		125
	Amino acids			X	125
	Glutamic acid			X	133

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
	Histidine	x			125,129,134
	Cysteine		X		125,135
	Other amino acids	X			129
	Cyclic AMP and other cyclic nucleotides	X			110,116,119,122,136-149,158
	High concentrations of cyclic AMP		X		116,137,150
	ATP and other nucleotide triphosphates	X			151,152
	Adenine, guanine		X		125,130
	Vitamins			X	125
	Folic acid & other pteridines	X			133,153
	Para-aminobenzoic acid			X	133
	Steroids	X			104, 154,155
	Steroids		X		156
	Diethylstilbestrol		X		132
	Progesterone		X		156-158
	Ionophore A 23187	X			158,159
	EDTA	X			157-159
	EDTA		X		160,161
	EDTA			X	128
	Inorganic salts (NaCl, $CaCl_2$, $MgCl_2$)	X			120,124,128-130,135, 160-163
	Ca^{2+}	X			116,124,128,135,139,140, 160-163

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
	Mg^{2+}	X			130,158,160-163
	Mn^{2+}, Zn^{2+}, Cu^{2+}	X			128
	Mg^{2+}, Ni^{2+}, Co^{2+}			X	128
b) Polysphondylium	Excess nutrients		X		164
	Casein	X			153
	Peptide acrasin	X			165
	Cyclic AMP			X	112,147
	Dibutyryl cAMP, cGMP, cAMP		X		150
	Glutamic acid			X	133,166
	Para-aminobenzoic acid			X	133,166
	Folic acid	X			133,153,166
	Pterin	X			166
	Other pteridines	X		X	133,166
	2,2-dichlorovinyldimethyl phosphate	X			167
	Acetylcholine	X			167
	Eserine	X			167
	Atropine		X		167
c) Acytostelium	No air		X		168
	Steroids	X			168
	Yohimbine tartarate and other alkaloids	X			168

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
III. Yeasts[169-171]					
I) Sexual agglutination in *Hansenula wingei*[169-173]	Yeast extract	X			173
	Malt extract		X		173
	Peptone, gelatin , protamine sulfate	X			174
	Glucose as energy source	X			173
	Glycerol as energy source		X		173
	Sorbose		X		173
	EDTA			X	174
	Cations (Mg^{2+}, Fe^{3+}, Cu^{2+}, Na^{+})	X			174,175
Diploid to 5	Aeration	X			173,176
	Excess aeration		X		177
	Exhaustion of medium	X			173,177
	Growth limiting	X			177
	Culture filtrate	X			177
	Yeast extract	X			173,176,177
	Minimal medium		X		173,176
	Peptone or Casamino acids			X	176
	Glucose as energy source	X			173,176
	Vitamin limitation	X			177
	Pyridoxine, biotin, thiamine	X			177

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
	Folic acid, para-aminobenzoic acid, inositol, niacin, riboflavin, pantothenate			X	177
	Adenine, guanine, cytosine, thymine, uracil		X		177
	Ca- + Mg-free medium	X			177
	Low Ca^{2+}, Mg^{2+}	X			176,177
	High Ca^{2+}, Mg^{2+}		X		177
	EDTA		X		176,177
	Vanadate	X			176,177
	Molybdate	X			176,177
	Tungstate	X			176,177
	Chromate		X		176
	Other cations (Co^{2+}, Cu^{+}, Cu^{2+}, Fe^{2+}, Fe^{3+}, Mn^{2+}, Ni^{2+}, Zn^{2+})			X	176
Diploid to 21	Aeration	X			177
	Yeast extract	X			177
	Trace element limitation	X			177
	Amino acid, excess vitamins to minimal medium		X		177
	EDTA	X			176,177
	Other chelators			X	176
	Metal ions		X		177
	Ca^{2+}		X		176

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
2) Sexual agglutination in	O_2	X			178
Kluyveromyces lactis	Ergosterol	X			178
	Squalene	X			178
3) Aggregate formation in	Nutrient limitation	X			179
Phialophora dermatitidis	Sabouraud dextrose agar + Czapek broth + yeast extract	X			179
4) Sex-directed flocculation in	Aeration	X			183-185,188
Schizosaccharomyces pombe[171,180-182]	Nutrient limitation	X			183-189
	Yeast extract		X		183-185
	Yeast nitrogen base		X		184,185
	Peptone	X			185
	Glucose		X		183,184,190
	Vitamin-free Casamino acids	X			185
	Aspartate		X		187
	Low cyclic AMP			X	190
	High cyclic AMP		X		190
	Salts	X			183,191
5) Sexual flocculation in	Yeast extract			X	192
Schizosaccharomyces japonicus	Glucose	X			192
	High glucose			X	192

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System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
6) Sexual agglutination in *Saccharomyces cerevisiae*[169-171,193]	Aeration	X			194-197
	Culture fluid	X			198
	Mating factor from α			X	199
	Peptidyl sex factor	X			198, 200-205
	α-factor			X	197
	α-factor		X		196
	Peptone	X			202
	No fermentable sugars (glucose, mannose, sucrose)		X		203
	Glucose	X			196,197,206,207
	Maltose or glycerol as C source		X		203
	Acetate		X		203
	Additional nucleoside bases			X	202
				X	217
7) Flocculation in brewers yeast[2,3,208-216]	Aeration	X			218
	Aeration	X			216,219-221
	Wort		X		217,222,223
	Wort	X			218
	Low-carbohydrate wort		X		218
	Maltose-rich wort		X		224
	Wort with high assimilable N		X		225
	Wort colloids				

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
	High-Mol.-Wt. wort fraction	X			220,221
	Barley gum malt β-glucan			X	220,221
	Polysaccharides in wort	X			226,227
	Araboxylan with proteins in wort	X			220,221
	Proteins in wort	X			228
	Proteins in wort		X		225,229
	Humic-acid-like compounds in wort	X			225,230,231
	Humic-acid-like compounds in wort			X	232
	Minimal medium (glucose, ammonium salt, vitamins, ions)		X		216
	Synthetic medium	X			222
	Peptone yeast extract	X			233
	Peptone			X	217
	Casein hydrolysate			X	217
	Acidic peptides in wort	X			216,219,234
	Basic peptides in wort			X	216,219,234
	Carbohydrates		X		208,217,222,229,235
	Sugar mixtures	X			218
	Fermentable sugars		X		213,229
	Glucose	X			236,237
	Glucose		X		229,233,235,238

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
	Glucose			X	239
	Maltose		X		217,222,229,235,238, 240,241
	Maltose			X	239
	Maltose	X			237
	Fructose		X	X	229,238,239
	Fructose	X			237
	Mannose		X		222,229,235,238,239,241,242
	Mannose	X			237
	Sucrose		X		208,217,229,235,238,241
	Sucrose	X			237
	Galactose			X	229,239
	Galactose		X		235,238
	Lactose			X	217,229
	Lactose		X		235,238
	D-arabinose		X		239
	L-arabinose			X	229,239
	Raffinose			X	235,239
	Xylose			X	229
	Ribose			X	235
	Sorbose		X		235
	Glucosamine	X			229
	Glucosamine		X		238
	Glucosamine			X	243

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
	Dextran			X	229
	Dextrin			X	235
	Arbutin, salicin, cellobiose, gluconic acid		X		235
	Aesculin, galacturonic acid, glucuronolactone, mannitol, dulcitol, inositol			X	235
	Assimilable N		X		218,224,236
	Amino acids	X			219,234
	Basic amino acids		X		243
	Lysine		X		224
	β-alanine, 2-chloro-4-aminobenzoic acid	X			243
	Aspartate	X			216
	L-aspartic acid, D-aspartic acid, L-glutamic acid, D-glutamic acid	X			219
	L-glutamine, L-asparagine, L-lysine, L-ornithine, γ-aminobutyrate		X		243
	DL-cysteine, L-asparagine, DL-tryptophan, glycine, DL-serine, DL-valire, L-lysine, L-proline			X	235
	DL-methionine, DL-threonine, L-serine, L-phenylalanine, DL-tryptophan, DL-tyrosine, DL-proline, L-histidine, glycine, L-α-alanine, DL-valine, DL-leucine			X	243

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
	Urea as N source		X		243
	Ammonium salt as N source		X		243,244
	Ethanol	X			223,238-241
	Methanol	X			238
	Methanol			X	239
	Other alcohols (isopropanol, n-butanol, isobutanol, 1:3-butylene glycol)	X			238,239
	Acetone	X			238,239
	Ethylene glycol, ethyl acetate, t-butanol, n-amyl alcohol, isoamyl alcohol			X	239
	Lactic acid			X	239
	Succinic acid			X	239
	Pantothenate, folic acid			X	243
	Thiamine, riboflavin, pyridoxine, niacin			X	244
	Para-aminobenzoic acid			X	243,244
	Inositol		X		244
	Phosphate			X	217
	Salts	X			238,239,245
	High salt concentration		X		246
	NaCl			X	239
	Anions (carbonate, phosphate, fluoride, oxalate)		X		229

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
	Diglycollate, citrate, EDTA		X		246
	EDTA		X		216,242,246
	Mg^{2+}	X			216,229,237,239,244,245,247-251
	Ca^{2+}	X			208,216,217,222,229,234,238,240,242,245-256
	Ca^{2+}			X	217,222,223,244,253
	Na^{+}		X		238,239,246
	Low $Na^{+} + K^{+}$	X			250
	High $Na^{+} + K^{+}$		X		250
	Divalent cations (Ni^{2+}, Mn^{2+}, Co^{2+}, Fe^{2+}, Zn^{2+}, Cd^{2+}, Cu^{2+}, Ba^{2+}, Sr^{2+})	X			216,218,229,239,241,248,250,251
	Uranyl ion, Ba^{2+}, Sr^{2+}		X		216,246
Filamentous fungi					
1) Strand formation[257-259] in					
a) Merulius lacrymans	Non-nutrient medium with food-base	X			260,261
	Non-nutrient medium, food-base removed		X		260
	Non-nutrient medium + fresh food-base		X		260
b) Helicobasidium purpureum	Added nutrients in agar	X			262
	Malt extract	X			262
c) Cultivated mushroom	Non-nutrient medium with food-base	X			263,264
	Low-nutrient medium	X			264
	Malt extract agar	X			263

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
2) Rhizomorph formation[257-259] in					
a) Armillaria mellea	Air	X			265
	Potato dextrose agar	X			265
	Malt extract + dextrose	X			266
	Excess dextrose		X		266,267
	Peptone	X			266
	Excess peptone		X		266
	3-5 parts of glucose to 1 of peptone or asparagine	X			267
	Excess asparagine		X		267
b) Marasmius androsaceus	Oatmeal agar compared to malt agar	X			268
3) Sclerotium formation[257-259,269-272] in					
a) Sclerotium	Low O_2 or high CO_2		X		272
	CO_2		X		273
	Transfer to fresh medium		X		274
	Medium for suboptimal growth	X			275
	High-nutrient medium		X		275-277
	Low-nutrient medium	X			276
	Onion agar	X			278
	Potato dextrose agar and oat meal agar compared to maize meal agar	X			279

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
	Glucose-nitrate agar	X			274
	Plain agar		X		274
	Varied sugars as C source			X	280
	Glucose as C source	X			277,279
	Glucose and sucrose as C source; compared to levulose, lactose, xylose, mannitol	X			279
	High glucose		X		275,277
	Increased C:N ratio	X			280
	Lactose	X			273,281,282
	Amino acids as N source	X			283
	L-threonine	X			273,282,283
	Phenylalanine	X			283
	L-cysteine		X		282,284-287
	Cystine		X		283,284,287,288
	Methionine		X		284,287
	Isoleucine, leucine, lysine		X		283
	L-homocystine, L-homocysteine thiolactone		X		284
	Glutathione		X		284
	Varied N sources (asparagine, peptone, nitrate, ammonium salt)			X	279,280
	Organic N	X			289

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
	Urea as N source		X		280
	Nitrate as N source	X			277
	High nitrate		X		277
	Ethanol		X		281,282,288,290
	Vitamins			X	280
	Thiamine	X			277, 291
	Iodoacetic acid		X		287
	Iodoacetic acid	X			273,282,284-286,288
	Potassium iodate	X			285
	Potassium iodate		X		287
	High phosphate		X		277
	Low dimethylsulfoxide	X			292
	High dimethylsulfoxide		X		292
	Other sulfoxides			X	292
	EDTA	X			285,286
	EDTA		X		287
	Mg^{2+}			X	277,285
	Cu^{2+}		X		285
	High K^{+}		X		277
	Ca^{2+}, Zn^{2+}, Co^{2+}, Mn^{2+}, Fe^{2+}, Mg^{2+}			X	277,285
b) Corticium rolfsii	Diamalt agar	X			293
	Mycelial extract	X			294-297

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
c) Sclerotinia	Carbohydrates	X			298,299
	Varied sugars as C source (glucose, fructose, lactose, maltose, sucrose, galactose)			X	280
	Increased glucose	X			280
	Raffinose, sucrose, maltose, lactose, D-mannose, D-glucose, D-fructose, L-arabinose as C source	X			300
	As C source: cellobiose, D-xylose, trehalose, melibiose, L-sorbose, L-rhamnose, D-ribose, D-arabinose, L-xylose		X		300
	As C source: D-mannitol, D-glucitol, L-arabitol, D-galactitol, xylitol, ribitol, glycerol		X		300
	Levulose, galactose, saccharose, lactose, dextrin, glycogen compared to glucose as C source			X	301
	Mannose, glycerol, soluble starch as C source		X		301
	Maltose	X			299

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
	Lactose, galactose		X		299
	Mannitol		X		299
	Amino acids as N source	X			302
	Asparagine as N source	X			298,302,303
	Ammonium N compared to nitrate, urea, glycine	X			299
	L-alanine, D-glutamine, L-glutamine, DL-glutamine, DL-serine, L-serine as N source	X			302
	β-alanine, D-alanine, L-cystine, L-cysteine, D-glutamic acid, D-methionine, D-leucine, D-serine		X		302
	DL-alanine, D-asparagine, D-aspartic acid, L-aspartic acid, L-glutamic acid, DL-leucine, L-leucine, DL-methionine, L-methionine compared to nitrate as N source		X		302
	Cystine	X			287
	Cysteine, methionine		X		287
	Varied N source (asparagine, peptone, nitrate, ammonium salt)			X	280

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
	Increased peptone as N source		X		280
	Urea as N source		X		280
	Urea as N source	X			298
	Ammonium salt & nitrate as N source	X			298
	Thiamine	X			280,304
	Pyridoxine	X			304
	Biotin	X			304
	Iodoacetic acid		X		287
	Potassium iodate	X			287
	High phosphate		X		298
	EDTA	X			287
	Zn^{2+}	X			287,303
	O_2	X			305
d) Aspergillus	Peptone	X			306
	Sucrose as C source	X			307
	Glucose as C source		X		307
	Glucose as C source	X			306
	Urea as N source		X		307
	Nitrate as N source	X			307

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
e) Rhizoctonia solani	Varied sugars as C source (glucose, fructose, sucrose, maltose, lactose, arabinose, starch)				
	Increased glucose or sucrose			X	280
	Varied N source (peptone, asparagine, nitrate, ammonium salt)	X			280
	Urea as N source			X	280
	Vitamins		X		280
f) Botrytis cinerea	Varied sugars as C source (glucose, fructose, sucrose, maltose, lactose, arabinose, starch)			X	280
	Increased glucose			X	280
	Varied N source (peptone, asparagine, nitrate, ammonium salt)	X			280
	Increased peptone			X	280
	Urea as N source	X			280
	Vitamins		X		280
g) Pyronema domesticum	Enriched medium (potato dextrcse agar or malt agar)			X	280
4) Microsclerotium formation in Verticillium	O_2	X			308
	Low nutrient medium	X			309
	Diffusible factor		X		310
		X			311,312

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
	Sucrose as C source	X			310,313
	Sucrose			X	311
	High C:N ratio	X			313
	High asparagine		X		310
	Ammonium sulfate as N source	X			313
	Nitrate as N source	X			310,313
	Nitrate, phosphate, sulfate			X	311
	Biotin, desbiotin	X			314
	Inositol, niacin, calcium pantothenate, pyridoxine, thiamine			X	314
	Mn^{2+}	X			311
	K^{+}, Fe^{3+}, Zn^{2+}, Mg^{2+}, Cu^{2+}			X	311
5) Synnema formation in					
a) Hirsutella gigantea	Varied sugars as C source			X	315,316
	N sources: liver fraction, autolysed yeast	X			315
	N sources: Neopeptone, Tryptone, yeast extract, casein hydrolysate		X		315
	Glutamic acid as N source		X		315
	High N		X		316
	Phosphoglyceric acid	X			315
	Gibberellic acid	X			315

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
b) Isaria cretacea	Starvation	X			317
	As C source: glucose, potassium gluconate sodium lactate, fructose, mannose, galactose, xylose, ribose, maltose, lactose, starch	X			316,318
	Sucrose		X		316-318
	Cellobiose		X		316,318
	Mannitol		X		316-318
	Sodium acetate		X		316,318
	High glucose		X		316
	Low C & N	X			316
	Varied N sources: ammonium salt, sodium nitrate, urea, tryptophan, glycine, valine, glutamic acid, asparagine, peptone, yeast extract			X	316-318
	High ammonium succinate as N scurce		X		316
	Vitamins			X	318
	Biotin, thiamine	X			316,317
	Indoleacetic acid & related auxins	X		X	316,317
	Selenite, cysteine, glutathione			X	316
	Phosphate	X			317
	Calcium carbonate	X			317

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
c) Graphium ulmi	Varied C sources			X	316
	High glucose		X		316
	Varied N sources: ammonium succinate, peptone, asparagine, glutamate, urea, yeast extract, glycine, L-tryptophan, L-valine			X	316
	High ammonium succinate as N source		X		316
	Indoleacetic acid & other auxins			X	316
	Selenite, cysteine, glutathione			X	316
6) Coremium formation in					
a) Penicillium	Malt agar compared to Czapek agar	X			319-321
	Amino acids compared to ammonium salt as N source			X	322
	Mg^{2+}-deficient minimal medium		X		322,323
	Mg^{2+}	X			322,323
b) Sphaerocybe concentrica	Thiamine	X			324
	Pyrimidine + thiazole	X			324
	Indoleacetic acid			X	324
V. Algae[325-334]					
1) Mating reaction or sexual agglutination in Chlamydomonas	Oxygen	X			335,336

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
	CO_2			X	335
	CO_2		X		336
	N_2			X	335
	Cell-free culture fluid	X			337
	Gamones	X			331,337-340
	Sugars			X	335
	Sucrose			X	341
	Mannose			X	340-342
	α-methyl-D-mannoside, α-methyl-D-galactoside			X	340
	N depletion	X			328,333,343-357
	Arginine			X	354,355
	Glutamine		X		344
	Glutamate		X		344
	Glycine			X	344
	Cysteine			X	335
	Ammonium salt		X		338,344,355
	Nitrate		X		338,344
	Urea		X		344
	Cyclic AMP	X			358
	AMP			X	358
	ATP			X	335

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
	Phosphoglycerate			X	335
	Succinate			X	335
	Acetate			X	325,335,338
	Low sodium acetate	X			359
	High sodium acetate		X		359
	Phosphate			X	325
	Citrate, oxalate	X	X	X	325
	Citrate		X		326
	Gibberellin A7	X			358
	EDTA		X		360
	Monovalent cations		X		338
	Divalent cations	X			326,360,361
	Ca^{2+}	X			326,360-362
	Mg^{2+}	X			326,360-362
2) Agglutination reaction in	Depletion of nutrients	X			363
Dunaliella salina	Saline	X			330,363
3) Isoagglutination of gametes in	N limitation	X			364
Pandorina	S limitation	X			364
	Cell-free culture fluid	X			330,365
	Vitamin B_{12}			X	364
	Trace metal mixture			X	364

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
	EDTA		X		364
	Ca^{2+}	X			364
	Mg^{2+}	X		X	364
4) Agglutination of gametes in *Ulva mutabilis*	Transfer to fresh growth medium	X			366-368
	Vitamins	X			366
VI. Protozoa[330,369-381]					
1) Mating reaction in *Blepharisma*	Starvation	X			381-383
	Cell-free culture fluid	X			10,381,384-386
	Blepharismone (gamone 2)	X			381,384,386-390
	Blepharmone (gamone 1)	X			383-386,388-390
	L-tryptophan, D-tryptophan	X			381
	L-hydroxytryptophan, D-hydroxytryptophan	X			381
	Glycine, alanine, serine, valire, thrconine, proline, histidine, phenylalanine			X	381
	Cyclic AMP			X	388
2) Mating reaction in *Euplotes*	Non-nutrient medium	X			381
	Well fed + exhausted food supply	X			391
	Decline in nutrient	X			391
	Cell-free culture fluid			X	11
	Sea water	X			11
	Ca^{2+}			X	11

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
3) Mating reaction in Paramecium	Dissolved gases	X			373
	Complete starvation		X		370-392
	Overfeeding		X		392,393
	Starvation after feeding	X			370,379,381,394
	Starvation in sterile tap water	X			395,396
	Culture fluid			X	397
	EDTA + $MgCl_2$	X			398
	Ca^{2+}			X	381
	Ca^{2+}	X			399,400
4) Mating-aggregate formation during chemically induced conjugation in Paramecium	Extreme starvation		X		401
	Cell-free culture medium		X		402
	Non-nutrient salt solution	X			403
	Ca-poor condition	X			401,404
	Heparin	X			401,404
	Cysteine HCl	X			402
	Formamide			X	401
	Acetamide	X			401-404
	Propanamide, malonamide	X			401
	Methanol			X	401
	Ethanol, propanol, butanol	X			401
	Glycerol	X			401

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
	Urea, methyl urea	X			401-404
	Picric acid			X	401
	Biuret	X			401-404
	Acriflavine, proflavine	X			401,402,404
	Acridine yellow, acridine red & related compounds	X			402,404
	Acridine orange			X	402
	EDTA	X			398,404,405
	Monovalent anions			X	403
	K^+, Na^+	X			401-404
	Mg^{2+}	X			401-404
	Mn^{2+}	X			404-406
	Ca^{2+}		X		401-404
	High Ca^{2+}	X			401, 403,407
	Co^{2+}	X			405
	Rb^+, Cs^+	X			401,408
	Be^{2+}, Sr^{2+}, Hg^{2+}			X	401
	Li^+, NH_4^+	X			401-403
	Ni^{2+}, Al^{3+}	X			403,409
	Hg^{2+}, Cu^{2+}, Cd^{2+}, Zn^{2+}			X	375
	KCl + acriflavine + Ca-poor condition	X			404,407,410
	Other cations	X			401

System & Review References	Nutritional condition	Positive	Negative	Indifferent	Reference
5) Clumping in Mayorella palestinensis	Anoxia		X		411
	Growth medium	X			411
	Peptone	X			411
	Agar		X		411
	EDTA			X	411
	High salt concentration		X		411

POOR

QUALITY

ORIGINAL